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THE INHERITANCE OF RESISTANCE TO PUCCINIA GRAMINIS TRITICI IN A CROSS BETWEEN TWO VARIETIES OF TRITICUM VULGARE[1]

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Wheat varieties that are susceptible to certain physiologic forms of *Puccinia graminis tritici* in the seedling stage often show very high resistance under field conditions. Hayes *et al.* (5) describe the inheritance of rust resistance in a cross of Marquis × Iumillo with Marquis and show that the Marquis × Iumillo resistance shown in the field is dependent on at least two genetic factors which are inherited apparently independently from a single factor for immunity from certain physiologic forms under greenhouse conditions. In this instance the resistance shown in the field is not necessarily a different type of resistance from that shown in the greenhouse. Physiologic forms other than the group to which the Marquis × Iumillo parent is immune were evidently present in the field, and the results indicate that a different set of factors were operating for resistance to these forms. Aamodt (1) points out that the reaction to particular physiologic forms shown by seedling plants in the greenhouse may not necessarily be a criterion of the reaction in the field and in addition gives an excellent review of published data on this phase of rust investigations. Aamodt states that, "Immunity or a high type of resistance can be differentiated in the seedling stage in the greenhouse with the expectation that the strains probably also will be resistant in the field. Moderate resistance, however, must be differentiated under field conditions in order to have an accurate determination of the reaction of the plant." The question as to the value of a greenhouse test for resistance is therefore left somewhat in doubt. In order to answer the question satisfactorily it is evident that tests conducted on plants approaching maturity must be carried out under conditions such that the physiologic forms may be controlled. The lack of agreement between field and greenhouse results may be due on the one hand to additional rust forms that are present in the field and on the other hand to the expression in plants approaching ma-

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turity of a type of resistance that cannot be detected in the seedling stage. An increasing resistance as the plants of certain strains mature does not necessarily indicate an increase in the physiologic resistance shown in the seedling stage but perhaps merely the superimposing of a mature plant type of resistance which may or may not be physiological.

The present study was undertaken in order to obtain further information on the inheritance of high degrees of both seedling and field resistance, and particularly on the relation between the two types of resistance.

PARENT MATERIAL

The resistant parent in the cross studied is known as H–44–24 and was produced by McFadden (7) by crossing Yaroslav emmer with Marquis wheat. This strain has been almost entirely free from rust during the past three seasons in tests conducted by the Botany Division at all of the experimental stations in Western Canada. Occasionally, small pustules may be found just above the nodes but it is quite certain that damage from rust is negligible. Agronomically, H–44–24 is probably not of much value since it is somewhat short and weak in the straw, has rather persistent glumes, and a slightly brittle rachis. As to the milling quality of the grain not much information is yet available but one test has been made

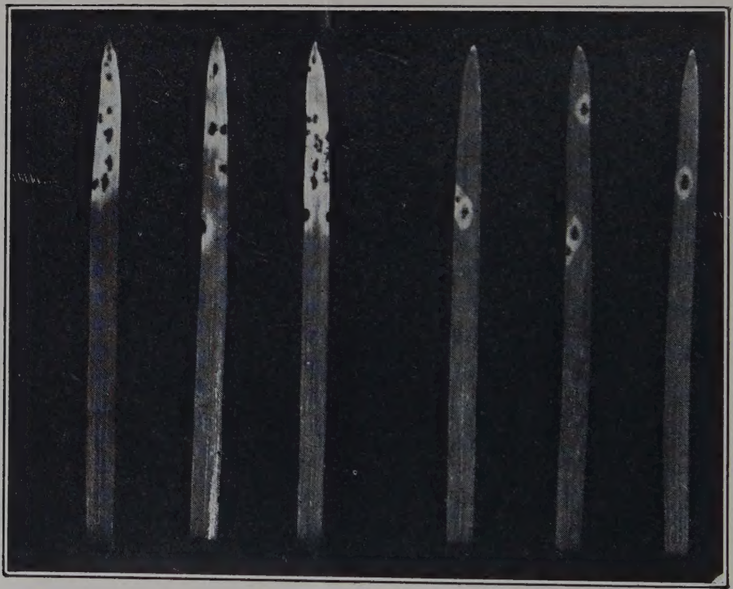

FIG. 1. Seedling reactions of Marquis (left) and H–44–24 (right) to physiologic form 21.

at the Cereal Division Milling and Baking Laboratory at Ottawa. From the standpoint of loaf volume, texture, and color of bread, the wheat was quite satisfactory. The crust was somewhat durum-like in character.

Seedling tests of H–44–24 for rust resistance to seven physiologic forms have been conducted by Newton and Johnson (8), and table 1 is an excerpt from their publication comparing the reactions of H–44–24 and Marquis.

TABLE 1.—*The reaction of H–44–24 and Marquis, common spring wheats, to seven physiologic forms of Puccinia graminis tritici*

Varieties	Host reaction to physiologic forms						
	21	29	30	32	34	36	+[a]
H–44–24, R.L. 229	2 +	2 +	3 –	—	—	0; 1	1
Marquis, R.L. 84	4	4 –	4	4 =	4 –	4	2 –

[a] An unidentified form.

The reactions of H–44–24 and Marquis to forms 21 and 36 are shown in figures 1 and 2.

Marquis was chosen as the other parent in the cross owing to its desirability, with the exception of rust reaction, for conditions in Western Canada.

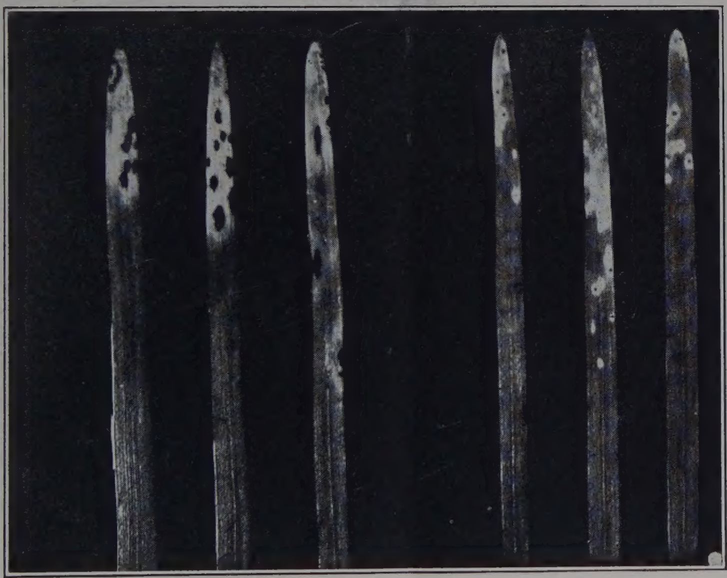

FIG. 2. Seedling reactions of Marquis (left) and H–44–24 (right) to physiologic form 36.

FIG. 3. Seedling reaction of F_1 plants of H–44–24 × Marquis to physiologic form 21.

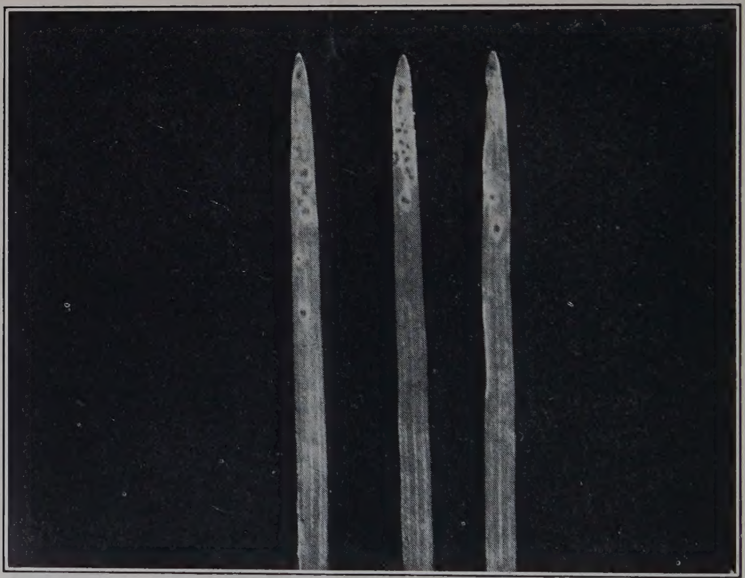

FIG. 4. Seedling reaction of F_1 plants of H–44–24 × Marquis to physiologic form 36.

THE F_1 GENERATION

The first generation plants were all grown in the greenhouse during the winter of 1925–26. Seedlings of F_1 plants were tested to the two forms 21 and 36 with results as shown in figures 3 and 4.

The moderate resistance of H–44–24 to form 21 is recessive in the F_1 while the high resistance to form 36 is dominant. As will be shown later this is supported by data on the seedling reactions of the F_3 families.

An interesting feature of the resistance of F_1 plants was observed when these were inoculated with form 21 at different stages of maturity. The results, as given in table 2, and illustrated in figure 5, show that seedling

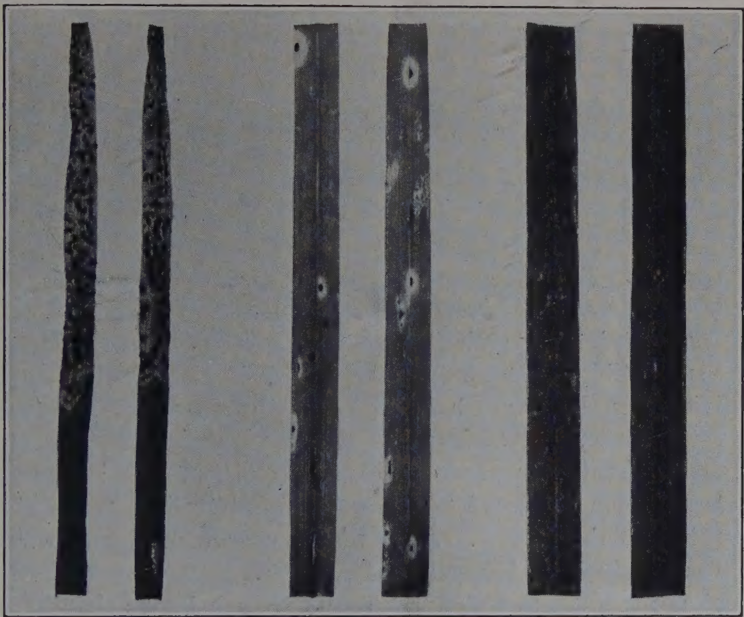

FIG. 5. Leaves from F_1 plants of H–44–24 × Marquis inoculated with physiologic form 21 at different stages of maturity. Left, seedling stage; centre, shot blade; right, fully headed.

susceptibility in this case changes very quickly to moderate resistance and by the time the plants are fully headed they show almost complete resistance. As evident from the table, each test was conducted in duplicate. This result indicated the possibility of the presence of factors for mature plant resistance which completely covered up the susceptibility evident only in the seedling stage.

TABLE 2.—*Rust reaction of F_1 plants of H–44–24 × Marquis at different stages of maturity, to physiologic form 21*

Date planted	Plot no.	Rust reaction on	
		Leaf	Culm
June 3	10	3 ++	—
	9	3 ++	—
May 20	8	2 ±	2
	7	2 ±	3c
May 6	6	2 –	3 ± c
	5	2 –	3 – c
April 22	4	1 –	1 – 2
	3	1	1 ±
April 8	2	0	1 –
	1	0	1 –

THE F_2 GENERATION

In 1926 a population of about 5000 F_2 plants was grown in the experimental field of the Dominion Rust Research Laboratory at Winnipeg, and an artificial rust epidemic was produced with the seven physiologic forms listed in table 1. The epidemic was a little late getting started, but sufficient rust was present to show that segregation was taking place in the mature plants of the F_2 population and that resistance was partially dominant over susceptibility. A random sample of 1054 plants was taken and the plants divided as they were harvested into three groups, R (resistant), SR (semi-resistant), and S (susceptible), the reaction being determined entirely from rust development on the stems and leaf sheaths. According to this classification the H–44–24 fell quite definitely into the R class and the Marquis into the S class. Assuming resistance dominant, the results are as given in table 3 and fitted to a 3 : 1 ratio.

The fit is not good to a 3 : 1 ratio but is much better than to a 15 : 1 ratio. This result was somewhat to be expected as the epidemic was not severe enough to differentiate between S and SR types. The numbers obtained in the three classes were R–301, SR–555, and S–198. The deficiency in the S class seems to have been added to the SR class and this is borne out by results on the F_3 families.

GREENHOUSE TESTS ON F_3 GENERATION FAMILIES

During the winter of 1926–27 portions of each F_3 family were tested to forms 36 and 21. The parent reactions shown in figures 1 and 2 have

TABLE 3.—*Segregation in the field of the F_2 population of H–44–24 × Marquis for resistance and susceptibility, and calculation of goodness of fit to a 3:1 ratio*

Groups	Actual	Theoretical (3:1)	Dev.	P.E.	$\frac{\text{Dev.}}{\text{P.E.}}$
Resistant and semi-resistant	856	790.5	65.5	9.48	6.91
Susceptible	198	273.5			

already been described. To form 36 the F_3 plants showed amounts of resistance varying from the resistance of H–44–24 to the susceptibility of Marquis. An intermediate type of resistance was also observed which was uniform in a number of lines. Three distinct reaction types are shown in figure 6. Since lines were obtained breeding true for the three distinct

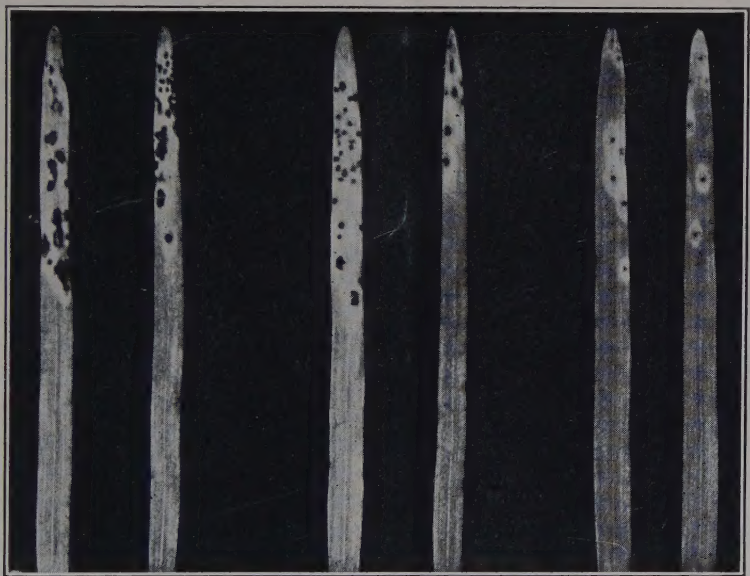

FIG. 6. Three degrees of resistance shown by F_3 lines of H–44–24 × Marquis to physiologic form 36. Left susceptible; centre, semi-resistant; right, resistant.

types, two factors governing the resistance to form 36 are indicated and this is borne out by a summary of the results from 745 F_3 families, the total number successfully tested to form 36. The families were classified according to their greenhouse reaction as homozygous susceptible, segregating, and homozygous resistant, and the data arranged as in table 4.

TABLE 4.—*Numbers of F_3 families of H–44–24 × Marquis classified by their greenhouse reaction as homozygous susceptible, segregating, and homozygous resistant to physiologic form 36.*

F_1 plant number	Number of F_3 families			Total no. families
	Homozygous susceptible	Segregating	Homozygous resistant	
550	0	38	12	50
538	2	44	8	54
535	5	50	13	68
534	7	31	9	47
543	13	29	10	52
541	6	36	17	59
537	3	40	4	47
551	4	13	5	22
548	1	23	1	25
533	0	11	1	12
542	1	34	11	46
545	2	50	13	65
546	0	25	11	36
549	1	19	5	25
539	2	7	1	10
540	2	36	10	48
547	0	23	4	27
544	0	39	13	52
Totals	49	548	148	745

It is evident that the ratio of homozygous susceptible families to the remainder is close to 1 : 15. The actual ratio is 49 : 696, and the theoretical 1 : 15 is 46.6 : 698.4. The deviation 2.4, divided by the probable error 4.46, gives 0.54, showing a very close fit.

The factor relations for resistance to form 36 in this cross are probably as illustrated in diagram 1.

In obtaining the actual data it was often very difficult to distinguish between homozygous R and SR types, so these have been added together in the summarized results as shown in table 5. (It was much easier to distinguish families segregating for R and SR.) The theoretical ratio for the three types is therefore 3 homozygous resistant, 12 segregating, and 1 homozygous susceptible. The comparison between actual and theoretical numbers is also given in table 5.

For three classes P = about 0.6 for $X^2 = 0.81$, Pearson (9), and Fisher (2). The fit is therefore very good.

The F_3 lines tested to form 21 were classified as homozygous resistant, segregating, and homozygous susceptible. By resistance in this case is

DIAGRAM 1. *Probable factor relations in the cross H–44–24 × Marquis for resistance in the seedling stage to form 36*

Parents .... H–44–24 – $R_1R_1R_2R_2$
Marquis – $r_1r_1r_2r_2$
F_1 .... $R_1r_1R_2r_2$

F_3	Theoretical frequency of genotypes	Genotypes	Phenotypes	Segregation in F_3
	1	RRRR	R	R
	2	RRRr	R	3R + 1SR
	2	RrRR	R	3R + 1SR
	4	RrRr	R	9R + 6SR + 1S
	1	rrRR	SR	SR
	1	RRrr	SR	SR
	2	Rrrr	SR	3SR + 1S
	2	rrRr	SR	3SR + 1S
	1	rrrr	S	S

TABLE 5.—*Numbers of F_3 families, homozygous resistant, segregating, and homozygous susceptible, to form 36, and calculation of goodness of fit to a theoretical 3:12:1 ratio*

Groups	Actual	Theor. (3:12:1)	$(A–T)^2/T$
Hom. R + SR	148	139.7	.49
Segregating	548	558.7	.20
Hom. S	49	46.6	.12
Totals	745	745.	$.81 = X^2$

meant the moderate resistance shown by the parent H–44–24 to form 21. The parental types recovered in the F_3 families are similar to those shown in figure 1. Aamodt (1) has referred to the reaction of H–44–24 to form 21 as moderately susceptible. This is perhaps a difference in terminology only. The term resistant was used in our case partly for convenience and partly on account of the hypersensitive areas around the pustules which led Newton and Johnson in 1927 to classify the reaction as 2+. Tests were conducted again in the fall of 1927 using form 21 on H–44–24 and many leaves showed a large number of small pustules without distinct hypersensitive areas. However, during the winter of 1926–27, when the F_3 families were tested, H–44–24 was used as a check and the reaction was consistently that shown in figure 1.

As might be expected, considerable difficulty was encountered in classifying the F_3 families but an attempt was made to make as careful a de-

termination as possible of the families breeding true for the reactions typical of the parents. The results are as shown in table 6.

TABLE 6.—*Numbers of F_3 families of H–44–24 × Marquis classified by their greenhouse reactions as homozygous susceptible, segregating, and homozygous resistant, to form 21*

F_1 plant no.	Number of F_3 families			Total no. families
	Homozygous susceptible	Segregating	Homozygous resistant	
550	7	9	4	20
535	6	9	4	19
534	10	26	5	41
543	12	19	5	36
541	31	16	7	54
537	9	33	8	50
551	30	39	5	74
548	14	38	4	56
533	16	27	2	45
542	16	26	9	51
545	14	40	8	62
546	23	27	1	51
549	14	6	2	22
539	17	26	7	50
540	18	33	2	53
547	10	24	4	38
544	17	42	2	61
Totals	264	440	79	783

Assuming susceptibility to the dominant as indicated by the F_1 reaction, the ratio obtained from the totals in table 6 does not give a good fit to either a 3:1 or 15:1 ratio. The goodness of fit is shown in table 7.

Since the fit is closest to a 15:1 ratio, it seems reasonable to assume a difference of two pairs of factors between the parents in this cross for moderate resistance to physiologic form 21.

GREENHOUSE TESTS ON F_4 GENERATION FAMILIES

Previous studies by other investigators, Puttick (10), Harrington and Aamodt (3), and Hayes and Aamodt (4), have demonstrated that the resistance of two varieties which react reciprocally to two physiologic forms of rust could be combined in a single variety. It is conceivable that in certain cases the factors governing high resistance to one or more forms may also govern a reaction to one or more other forms and the latter may be only moderate resistance or perhaps susceptibility. In the present study some indications have been obtained that this is actually the case. Fourteen F_4 lines which were known to be breeding true for high resistance to

TABLE 7.—*Numbers of F_3 families falling into the two classes, homozygous susceptible and segregating, and homozygous resistant, and calculation of the goodness of fit to 3:1 and 15:1 ratios*

Ratio	Actual		Theoretical		Dev.	P.E.	$\frac{\text{Dev.}}{\text{P.E.}}$
	Susc. and segregating	Resistant	Susc. and segregating	Resistant			
3:1	704	79	587.2	195.8	116.8	8.17	14.3
15:1	704	79	734.1	48.9	30.1	4.57	6.3

form 36 and moderate resistance to form 21 were tested in the seedling stage to seven forms, 9, 14, 15, 17, 21, 34, and 36. These all gave reactions similar to those of the H–44–24 parent. Eight F_4 lines breeding true for susceptibility to forms 21 and 36 were also tested to forms 9, 14, 15, 17, and 34. These all gave reactions similar to the Marquis parent including high resistance to form 14. The results are summarized in table 8.

TABLE 8.—*Reaction of twenty-two selected F_3 lines of H–44–24 × Marquis to seven physiologic forms of P. graminis tritici*

Field reaction	Strain no.	Physiologic forms						
		9	14	15	17	21	34	36
Susc.	7	2 3 –	2 3	3 +-	2 + 3 –	2 3	2 3	
	204	2	2 3	3 +-	2	2 3 –	2 3	1
	293	2 3 –	2 3	3 +	2 + 3 –	2 3	3 – 3	1
	456	2 + 3 –	2 –: 1	3 +-	3 –	2 3	2 3	1
	572	3	2 3	3	2 +	2 3	2 3	1
	587	3	2 3	3 +	2 +	2 3	2 3	1
	885	2 + 3 –	2 3 –	2 + 3	2	2 3	2 3	1
	937	3 +	2 3	3 +	3 –	3 –	3 –	1
Res.	128	2 3 –	2 3	3 +	2 3	2 3	2 3	1 –
	386	2 3 +	2 3	3 +	3	2 3	3 +-	1 –
	725	2 3		3 +	2 3	2 3	2 3	1 –
	880	2 3	2 3	3 +	2 3	2 3	2 3	1
	888		2 3	3 +-	3	2 3	3	1 –
	903	2 3	2 3 +	3 +-	2 3	2 3	2 3	1 –
Res.	99	4	1 –	4	3 +-		3 +	
	148	3 +	1	3 +	3 +		3 +	
	179	3 +	1	4	3 +		3 +	
	208	4	1	4	4		4	
	221		1	4 +	3 +		3 +	
	331	3 +	1	3 +-	3 +		3 +	
	450	3 4 –	1 +	3 +	3		3 +	
	875	4	1	4	4 –		3 +	

In this test only those lines were used which were either homozygous resistant or susceptible to both forms, 21 and 36, so it was impossible to determine whether the factors governing resistance to 21 or those governing resistance to 36 were also responsible or closely linked to factors governing resistance to the other forms. A further test was conducted on a group of twelve miscellaneous strains which were varied in their reactions to both forms. The results of this test are presented in table 9. It will

TABLE 9.—*Seedling reactions*[a] *of twelve miscellaneous* F_4 *lines of H–44–24 × Marquis, to physiologic forms 21, 14, 17, and 36*

Strain no.	Physiologic forms			
	21	14	17	36
105	Hom. MR	Seg. MR + R	Seg. S + MR	Seg. MS + R
125	Seg. S + MR	Seg. MR + R	Seg. S + MR	Seg. MS + R
248	Seg. S + MR	Seg. MR + R	Seg. S + MR	Hom. R
268	Hom. S	Hom. R	Seg. S + MR	Hom. R
323		Hom. R	Seg. S + MR	Seg. MS + R
349	Seg. S + MR	Seg. MR + R	Seg. S + MR	Hom. R
374	Hom. S	Hom. R	Hom. S	Seg. MS + R
431	Seg. S + MR	Seg. MR + R	Seg. S + MR	Seg. MS + R
490	Hom. S	Hom. R	Hom. S	Seg. MS + R
503	Seg. S + MR	Seg. MR + R	Hom. MR	Seg. MS + MR
504	Hom. MR	Hom. MR	Hom. MR	Seg. MS + R
859	Seg. S + MR	Seg. MR + R	Seg. S + MR	Hom. R

[a] S = (3 + and 4 reactions)
MS = (3 – and 3 reactions)
MR = (2 + and 3 reactions)
R = (1 – and 2 reactions)

be observed that there is a close reciprocal relation between the reactions of all but one of the strains to forms 21 and 14. No such relation exists between the reactions to forms 36 and 14. The data with respect to form 17 are not conclusive. Strains numbers 105 to 349 were read before the rust had developed sufficiently to give accurate results. On the remainder, numbers 374 to 859, the results agree quite well with those obtained for form 21. There seem sufficient data to show that in H–44–24 either the same factors govern the reaction to forms 21, 14, and 17, or if these factors are different they are closely linked. The factors for resistance to form 36 are distinct from those governing resistance to the other group of forms. One of the most interesting observations in this connection is the reciprocal relationship between the inheritance of resistance to forms 21 and 14. The Marquis factor or factors for high resistance to form 14 are allelomorphic

to H–44–24 factors for moderate resistance to form 21. In Marquis also the same factors give complete susceptibility to at least two other forms. The factor relationships in the two parents for rust reaction to forms 9, 14, 15, 17, 21, and 34, may easily be as indicated in diagram 2.

DIAGRAM 2. *Hypothetical factor relationships in H–44–24 and Marquis for resistance to physiologic forms 9, 14, 15, 17, 21, and 34.*

H–44–24		*Marquis*	
RR	MR– 9	rr	S– 9
	MR–14		R–14
	MS–15		S–15
	MR–17		S–17
	MR–21		S–21
	MR–34		S–34

If diagram 2 gives a true indication of the relation, it is impossible in this cross to combine the moderate resistance of H–44–24 to form 21 with the high resistance of Marquis to form 14.

It is evident from these results that the building up of resistance by hybridization must be carried out with extreme care in the matter of selection of parents and testing of the progeny to different physiologic forms. The first essential is a thorough genetic analysis of various parents with respect to the factors controlling resistance to different groups of forms. Not until these data have been obtained can a systematic program be outlined to build up resistance to a large number of forms in one variety.

FIELD REACTION OF F_3 FAMILIES

In the summer of 1927 the hybrid nursery was located at Morden, Manitoba, on the plots of the Dominion Experimental Station. The season was very late. Sowing was not completed until June 15. The natural epidemic was very heavy and all of the physiologic forms being carried in the greenhouse were transferred in pots to the field. The result was a very heavy epidemic, which practically destroyed all of the very susceptible varieties and strains.

The 1054 F_3 lines which had been tested the previous winter to forms 36 and 21 were all grown in the field. The parents were scattered uniformly throughout this nursery and, while Marquis was very heavily rusted and produced only very shrunken grain, H–44–24 was almost entirely free and developed normally with the exception of damage caused by foot rots. It did not appear to be more susceptible to such diseases, however, than other standard varieties.

About September 10 data were taken on the reaction of the F_3 lines to rust. They were classified while standing in the field as homozygous resistant, segregating, and homozygous susceptible. The segregation as

illustrated in figure 7 was so clear cut that this classification was easily made. The uniformly susceptible lines were very obvious. The results of this study are given in table 10.

If field resistance is governed by a single factor pair, the three classes should be obtained in a 1 : 2 : 1 ratio. The goodness of fit of the numbers obtained to the theoretical 1 : 2 : 1 is given in table 11.

This is not a satisfactory fit, owing to a deficiency in the resistant class which is added to the segregating class. There is a possibility that natural

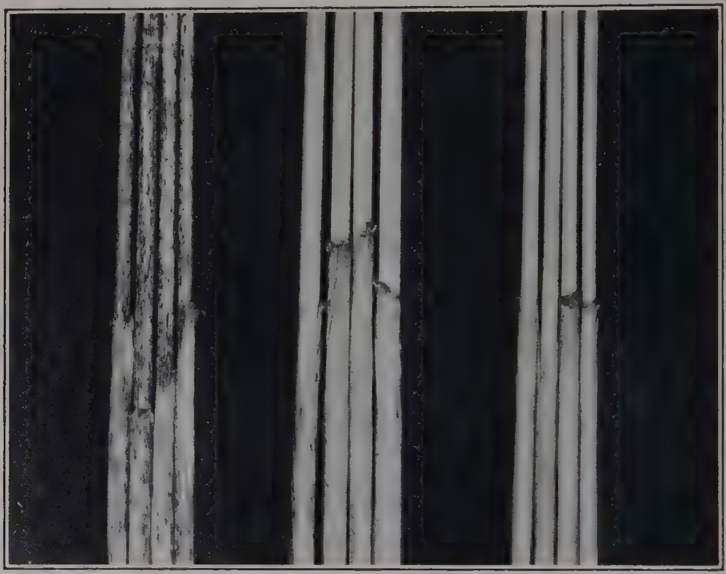

FIG. 7. Field reactions in 1927 hybrid nursery. Marquis, left; H–44–24, right; and a resistant F_3 line, centre.

crossing in the previous generation may have helped to produce such a result. Adding the resistant and segregating classes together, we get 796 : 249, which is a very good fit to a 3 : 1 ratio.

RELATION BETWEEN FIELD AND GREENHOUSE RESISTANCE

Any relation between field and greenhouse resistance should be most evident from a study of the families homozygous according to the greenhouse test for resistance or susceptibility to both of the rust forms used. There were 36 of such families susceptible in the seedling stage and 32 resistant. The segregation of these families for rust resistance in the field was studied in detail and the results are as given in table 12. It is evident

TABLE 10.—*Number of F_3 families homozygous resistant, segregating, and homozygous susceptible, as determined by the field reaction*

F_1 plant number	Number of F_3 families			Total
	Resistant	Segregating	Susceptible	
550	17	32	9	58
538	20	33	15	68
535	13	35	16	64
534	8	24	15	47
543	9	29	11	49
541	17	27	17	61
537	18	28	14	60
551	17	52	20	89
548	14	46	12	72
533	3	29	15	47
542	15	27	13	55
545	13	43	13	69
549	3	18	8	29
546	10	30	18	58
539	17	27	13	57
547	9	26	8	43
540	7	38	12	57
544	16	26	20	62
Totals	226	570	249	1045

that in both groups there is a 1:2:1 ratio of resistant, segregating, and susceptible families showing complete independence of the greenhouse test. The results are best summarized in the form of a 2-by-3-fold correlation surface, table 13, for which the calculated value of X^2 is 0.275. For $n=2$ (number of degrees of freedom) P is 0.90 to 0.80 indicating complete independence of the two distributions.

Irrespective of this result it cannot be definitely stated that there is not an observable relation between the two types of resistance. There is a

TABLE 11.—*Total number of F_3 families classified for field resistance as resistant, segregating, and susceptible, and calculation of the goodness of fit to a 1:2:1 ratio*

Actual numbers	Theor. numbers	$(A-T)^2/T$
226	261.25	4.756
570	522.50	4.318
249	261.25	.574
1045	1045	$9.648=X^2$ P = less than .01, Fisher (2)

distinct difference in the type of segregation in the two groups as shown in table 12. Families in the seedling-susceptible group segregate in the field approximately in a 1:2:1 ratio of resistant, semi-resistant, and sus-

TABLE 12.—*Segregation in the field for rust reaction of two groups of F_3 families*

Homozygous susceptible in seedling stage to forms 21 and 36				Homozygous resistant in seedling stage to forms 21 and 36			
Family no.	Resistant	Semi-resistant	Susceptible	Family no.	Resistant	Semi-resistant	Susceptible
100	All			129	All		
152	do			395	do		
183	do			733	do		
214	do			888	do		
227	do			896	do		
340	do			911	do		
459	do						
883	do						
75	0	40	17	24	27	10	14
256	15	18	10	191	27	1	6
292	2	18	7	278	12	2	10
295	9	23	6	348	14	22	11
419	0	38	17	467	28	6	10
421	3	22	5	560	35	0	15
423	12	41	17	631	47	0	12
470	6	19	8	666	79	2	29
471	20	46	19	670	52	0	20
473	5	23	12	706	29	0	7
615	17	34	13	718	33	0	17
619	10	24	19	719	39	0	9
829	19	35	28	782	64	1	9
836	22	31	18	988	34	8	11
841	14	14	7	192	Segregating nos. small		
854	14	15	13	283		do	
913	29	29	20	285		do	
984	4	30	17	502		do	
104			All	7			All
155			do	210			do
161			do	302			do
164			do	465			do
233			do	580			do
311			do	595			do
347			do	893			do
621			do	944			do
623			do				
748			do				

ceptible plants, while in the seedling-resistant group semi-resistant plants are almost completely absent. An explanation of this is not possible until a more detailed study has been made of the nature of resistance exhibited only by plants approaching maturity. If such resistance is purely morphological the results obtained from the segregation of these families are probably to be expected. It will be remembered that the SR class contains plants practically free from rust but usually with a few pustules on each plant just above the nodes, and in families susceptible in the seedling stage and segregating for resistance in the field the SR plants would be those heterozygous for the factor for morphological resistance which is not completely dominant. In families resistant in the seedling stage to at least two predominating forms, the chances of the development of rust on only a small portion of the plant surface would be much less, and the SR

TABLE 13.—*Two by three fold correlation tables summarizing results from table 12*

Field reaction / Seedling reaction	Homozygous resistant	Segregating	Homozygous susceptible	Totals
Resistant to forms 36, 21	8	18	10	36
Susceptible to forms 36, 21	6	18	8	32
Totals	14	36	18	68

$X^2 = 0.275$. $P = .90$ to $.80$.

class would be accordingly much smaller. In a plant showing only morphological resistance, as described by Hursh (6), there would seem to be greater chances of infection just above the nodes than on any other part of the plant, owing to the fact that the bundles coming out of the node have at that point not extended to the epidermis of the stem.

The exact nature of the resistance here referred to as field resistance is very important. Such families as numbers 100 to 883 in the seedling-susceptible group and numbers 129 to 911 in the seedling-resistant group are indistinguishable from the standpoint of resistance in the field. They are almost entirely free from rust, and if the type of resistance that they show is morphologic they would be expected to show this resistance irrespective of physiologic forms. It is a very pronounced type of resistance and, since it appears to be governed by only a single pair of factors, is extremely important from the plant-breeding standpoint.

GENETIC STUDIES ON OTHER CHARACTERS

Awning

Figure 8 illustrates the spike characters of H–44–24 and Marquis. In F_1 the type was almost intermediate but resembled Marquis more closely than the H–44–24 parent. In F_2 the ratio of awnless and intermediate to awned was 791 : 267. The deviation from a perfect 3 : 1 ratio is only 2.5 while the probable error is 9.5. This is a very close fit, and the classification of the F_2 plants was checked by the segregation in F_3 families.

FIG. 8.—Spikes of Marquis (left), H–44–24 (right), and F_1 plant (centre).

Persistence of Glumes

The F_2 plants were threshed with a machine made especially for single plant work. It consists of a drum covered with corrugated rubber which operates against a belt of corrugated rubber extending over about five inches of the circumference of the drum. The belt may be adjusted for tightness against the drum. The heads of a single wheat plant of the ordinary free threshing type are threshed in a few seconds by passing them between the rotating drum and the rubber belt. In threshing the plants in this cross it was observed that there was a fairly clear-cut differentiation between the free threshing Marquis type and the type with persistent glumes resembling H–44–24. The former were threshed by passing them

through the machine once while the others required passing through two to four times. Records were kept, therefore, on the remainder of the plants and a ratio of 540 persistent- to 154 free-threshing plants was obtained. Fitting this to a theoretical 3:1 ratio we have a deviation from the theoretical of 19.5 and a probable error of 7.69. The deviation divided by the probable error is 2.54, indicating that the departure from a 3:1 ratio is not particularly significant.

Pigmentation of Seedlings[3]

The seedlings grown in the greenhouse for tests of resistance to rust were examined for coloration when about one inch above the ground. A fairly definite segregation was observed and records were kept of the number of families breeding true for color, segregating, and breeding true for absence of color. The ratio obtained was 413:550:54. On the basis of a differentiation between the parents for this character of two pairs of factors the ratio to be expected would be as follows—

7 breed true for color
8 segregate
1 breeds true for absence of color

The goodness of fit of the actual to this theoretical ratio is shown in table 14.

TABLE 14.—*Number of F_3 families breeding true for color, segregating, and breeding true for absence of color, and goodness of fit to a theoretical 7:8:1 ratio*

Groups	Actual	Theor. 7:8:1	$(A-T)^2/T$
Colored	413	444.9	2.29
Segregating	550	508.5	3.39
Green	54	63.6	1.45
Total	1017	1017	$7.13 = X^2$ $P = .028$

Since P is less than 0.05 the deviation is quite significant. Table 14 shows that the big discrepancy is in the first two classes, the segregating class being much too large. The only class that was perfectly distinct was the homozygous green class. In the uniform pigmented classes a considerable variation due to environmental influences seemed evident so that a number of these may have been classed as segregating. The ratio of homozygous green families to the remainder is 54:963. The theoretical

[3] The coleoptiles of H–44–24 seedlings are of a distinct purplish red color.

1 : 15 ratio is 63.6 : 953.4. The fit here is good since the deviation from the theoretical is only 9.6 and the probable error is 5.21. It seems safe to conclude that the pigmentation of the seedlings is governed by two pairs of duplicate factors.

SUMMARY OF FACTOR RELATIONSHIPS

Putting aside for the present the possibility of linkage between any of the factors concerned, table 15 is a fairly accurate statement of the factor relations in the cross studied.

TABLE 15.—*A summary of factor relationships in the cross, H–44–24 × Marquis*

H–44–24		Marquis	
Factor	Character	Factor	Character
R_m	Resistance of mature plants to stem rust	r_m	Susceptibility of mature plants to stem rust
R_1R_2	Resistance to form 36	r_1r_2	Susceptibility to form 36
s_1s_2	do 21	S_1S_2	do 21
a	Presence of full awns	A	Absence of full awns
G	Persistence of glumes	g	Free threshing
P_1P_2	Pigmentation of seedlings	p_1p_2	Green seedlings

$R_mR_mR_1R_1R_2R_2s_1s_1s_2s_2aaGGP_1P_1P_2P_2 \times r_mr_mr_1r_1r_2r_2S_1S_1S_2S_2AAggp_1p_1p_2p_2$

THE INHERITANCE OF MATURE PLANT RUST RESISTANCE IN RELATION TO MORPHOLOGICAL AND OTHER CHARACTERS

As previously pointed out, the parent H–44–24 is a vulgare wheat derived from an emmer × Marquis cross. It carries with it in addition to rust resistance other characters derived from the emmer parent. It is bearded, has very persistent glumes, and the coleoptile when just emerging and until the plant is several days old is distinctly of a purplish red color. In these three characters it is sharply contrasted with Marquis. If only a few entire emmer chromosomes were transferred to H–44–24 there would seem to be considerable likelihood of an observable linkage between some of these characters. The segregation for these characters was therefore studied in some detail and an attempt made to detect any tendency for a pair of characters to be inherited together.

The method of measuring such relationships is shown in tables 16 to 30. These are contingency tables in each of which a pair of characters are considered. A direct measure of the relationship between the distribution for the two characters may be obtained by calculating X^2 and determining the value of P from Pearson's tables (9). In determining P from the tables,

Fisher's (2) suggestion has been followed relative to the number of degrees of freedom. Thus in a 3-by-3-fold table there are four degrees of freedom, and one enters Pearson's tables under $n = 5$. A summary of the values of P is given in table 31. In interpreting these results it is safe to assume that, if the value of P for any given distribution is higher than 0.05, there is no significant evidence of correlated inheritance. A P of 0.05 means that any association that exists between the two distributions might occur by chance in one out of twenty cases.

TABLE 16.—*Distribution of F_3 families for awning and field rust reaction*

Field rust reaction	Awned	Awning Segregating	Awnless	Totals
Res.	57	117	51	225
Seg.	149	291	127	567
Susc.	57	118	70	245
Totals	263	526	248	1037

$X^2 = 3.97$ $P = 0.411$

TABLE 17.—*Distribution of F_3 families for awning and seedling reaction to form 36*

Seedling reaction to form 36	Awned	Awning[a] Segregating	Awnless	Totals
Susc.	13	13	23	49
Seg.	130	213	203	546
Res.	35	67	46	148
Totals	178	293	272	743

$X^2 = 6.24$ $P = 0.184$

[a] Data taken on F_2 plants only. The class here referred to as segregating is represented by intermediate-type F_2 plants.

TABLE 18.—*Distribution of F_3 families for awning and seedling reaction to form 21*

Seedling reaction to form 21	Awned	Awning[a] Segregating	Awnless	Totals
Susc.	67	100	96	263
Seg.	116	186	138	440
Res.	18	34	27	79
Totals	201	320	261	782

$X^2 = 2.49$ $P = 0.649$

[a] Data taken on F_2 plants only. The class here referred to as segregating is represented by intermediate-type F_2 plants.

TABLE 19.—*Distribution of F_2 plants for awning and persistence of glumes*

Persistence of glumes	Awned	Awning Intermediate	Awnless	Totals
Per.	42	60	52	154
Int.	98	133	112	343
Free	42	90	65	197
Totals	182	283	229	694

$X^2 = 4.26$ $P = 0.375$

TABLE 20.—*Distribution of F_3 families for awning and cotyledon color*

Cotyledon color	Awned	Awning[a] Segregating	Awnless	Totals
Pig.	98	131	138	367
Seg.	128	195	175	498
Green	9	26	19	54
Totals	235	352	332	919

$X^2 = 4.34$ $P = 0.366$

[a] Data taken on F_2 plants only. The class referred to here as segregating is represented by intermediate-type F_2 plants.

TABLE 21.—*Distribution of F_3 families for seedling reaction to forms 21 and 36*

Seedling reaction to form 21	Seedling reaction to form 36			Totals
	Susceptible	Segregating	Resistant	
Susc.	14	113	41	168
Seg.	15	206	53	274
Res.	1	40	18	59
Totals	30	359	112	501

$X^2 = 7.69$ $P = 0.106$

TABLE 22.—*Distribution of F_2 families for persistance of glumes and seedling reaction to form 36*

Seedling reaction to form 36	Persistence of glumes[a] Persistent	Segregating	Free	Totals
Susc.	7	11	9	27
Seg.	57	144	92	293
Res.	15	40	26	81
Totals	79	195	127	401

$X^2 = 1.01$ $P = 0.908$

[a] Data taken on F_2 plants only. The class here referred to as segregating is represented by intermediate-type F_2 plants.

TABLE 23.—*Distribution of F_3 families for cotyledon color and seedling reaction to form 36*

Seedling reaction to form 36	Cotyledon color Pigmented	Segregating	Green	Totals
Susc.	21	27	1	49
Seg.	219	294	35	548
Res.	59	79	10	148
Totals	299	400	46	745

$X^2 = 1.59$ $P = 0.807$

TABLE 24.—*Distribution of F_3 families for persistence of glumes and cotyledon color*

Cotyledon color	Persistence of glumes[a] Persistent	Segregating	Free	Totals
Pig.	52	122	61	235
Seg.	60	146	90	296
Green	6	14	14	34
Totals	118	282	165	565

$X^2 = 3.82$ $P = 0.433$

[a] Data taken on F_2 plants only. The class referred to here as segregating is represented by intermediate-type F_2 plants.

TABLE 25.—*Distribution of F_3 families for seedling reaction to form 36 and field rust reaction*

Field rust reaction	Seedling reaction to form 36: Resistant	Segregating	Susceptible	Totals
Res.	51	157	12	220
Seg.	131	395	35	561
Susc.	58	162	22	242
Totals	240	714	69	1023

$X^2 = 3.16$ $P = 0.534$

TABLE 26.—*Distribution of F_3 families for seedling reaction to form 21, and field rust reaction*

Field rust reaction	Seedling reaction to form 21: Resistant	Segregating	Susceptible	Totals
Res.	25	105	64	194
Seg.	47	284	190	521
Susc.	21	120	77	218
Totals	93	509	331	933

$X^2 = 2.65$ $P = 0.620$

TABLE 27.—*Distribution of F_3 families for persistence of glumes and field rust reaction*

Field rust reaction	Persistence of glumes[a]: Resistant	Segregating	Free	Totals
Res.	35	72	35	142
Seg.	86	192	112	390
Susc.	34	81	51	166
Totals	155	345	198	698

$X^2 = 1.69$ $P = 0.790$

[a] Data on persistence of glumes were taken on F_2 plants. The class here referred to as segregating came from intermediate plants.

TABLE 28.—*Distribution of F_3 families for cotyledon color and field rust reaction*

Field rust reaction	Cotyledon color: Pigmented	Segregating	Green	Totals
Res.	87	126	11	224
Seg.	228	310	31	569
Susc.	101	140	7	248
Totals	416	576	49	1041

$X^2 = 2.82$ $P = 0.590$

TABLE 29.—*Distribution of F_3 families for persistence of glumes and reaction of seedlings to form 21*

Seedling reaction to form 21	Persistence of glumes[a]: Persistent	Segregating	Free	Totals
Susc.	49	96	52	197
Seg.	66	188	103	357
Res.	17	20	16	53
Totals	132	304	171	607

$X^2 = 7.73$ $P = 0.104$

[a] Data taken on F_2 plants only. The class referred to here as segregating is represented by intermediate F_2 plants.

TABLE 30.—*Distribution of F_3 families for cotyledon color and seedling reaction to form 21*

Seedling reaction to form 21	Cotyledon color: Pigmented	Segregating	Green	Totals
Susc.	105	144	14	263
Seg.	172	248	19	439
Res.	33	43	3	79
Totals	310	435	36	781

$X^2 = 0.71$ $P = 0.936$

TABLE 31.—*Summary of values of X^2 and P from tables 16 to 30*

Table	Characters[a]	X^2	P	Table	Characters	X^2	P
16	AM	3.97	0.411	25	MR_1	3.16	0.534
17	AR_1	6.24	0.184	26	MR_2	2.65	0.620
18	AR_2	2.49	0.649	27	MG	1.69	0.790
19	AG	4.26	0.375	28	MP	2.82	0.590
20	AP	4.34	0.366	29	R_2G	7.73	0.104
21	R_1R_2	7.69	0.106	30	R_2P	0.71	0.936
22	R_1G	1.01	0.908				
23	R_1P	1.59	0.807				
24	GP	3.82	0.433				

[a] Explanations of symbols:

A—awning
G—persistence of glumes
P—Cotyledon color
R_1—seedling resistance to form 36
R_2—seedling resistance to form 21
M—mature plant resistance

Linkages are of course very difficult to detect when one or both of the characters are governed by two pairs of factors, but with regard to the characters represented by A, M, and G the results would appear to be quite conclusive.

DISCUSSION

The existence in such a variety as H–44–24 of a type of rust resistance which does not become evident until the plants are about half way to maturity is of particular significance from the standpoint of breeding work. It appears to be a very pronounced type of resistance amounting almost to immunity and, while there is no definite evidence to the effect that it reacts in the same manner to all physiologic forms, there seems good reason to believe that it does react in the same manner to all of the forms commonly found in the Northwest. From the breeding standpoint, therefore, this entire group of forms may perhaps be considered as an entity. This considerably simplifies the problem especially since we seem to have fairly good evidence that the type of resistance referred to its governed by only a single pair of factors.

Whatever may be the practical value of the results reported here, it is evident that in all breeding problems studies of the inheritance of rust resistance should take into consideration both the seedling reactions and the mature plant reactions of the parents to different physiologic forms. If a mature-plant type of resistance exists in one or both of the parents, it is obvious that a close agreement between seedling and field results is not to be expected.

SUMMARY

1. A cross was made between H–44–24, a vulgare derivative from a Marquis × emmer cross, and Marquis.

2. The H–44–24 parent is moderately resistant in the seedling stage to several forms of *Puccinia graminis tritici*, including forms 14 and 21, and highly resistant to form 36. Marquis is susceptible to a large number of forms, including forms 36 and 21, but is highly resistant to form 14.

3. The high resistance of H–44–24 to form 36 is dominant in the F_1 generation but its moderate resistance to form 21 is recessive. Tests on 1000 F_3 families clearly indicated that there is a difference between the parents of two pairs of factors for resistance to form 36, and the same is probably true for resistance to form 21.

4. Studies of the reactions of F_4 lines breeding true for reactions to forms 21 and 36 showed that all of the lines possessing moderate resistance to form 21 gave the same reaction as Marquis to this group of other forms. This group of forms contains form 14 to which Marquis is highly resistant and others such as 21 and 17 to which it is highly susceptible. It would seem that in this case the same factors govern resistance to one form and susceptibility to another.

5. First generation plants susceptible to form 21 in the seedling stage showed very high resistance to the same form as they approached maturity. Studies of the field reaction of one group of F_3 lines breeding true for susceptibility in the seedling stage to forms 21 and 36 and of another group breeding true for resistance to forms 21 and 36 showed that segregation in the field was quite independent. The field results indicated that resistance in the field is controlled by a single pair of factors only.

6. An attempt was made to detect any tendency towards linkage in the inheritance of mature plant resistance, seedling resistance to form 21, seedling resistance to form 36, awning, persistence of the glumes, and cotyledon color. No such tendency was observed.

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